Deep-Diving California Sea Lions:
Are they pushing their physiological limit?

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LONG-TERM GOALS

The 500-m diving capacity of the California sea lion (*Zalophus californianus*) represents a model in which a generally considered shallow-diving species is potentially approaching its physiological limit during dives greater than 300 m in depth. The physiology of these extreme dives is relevant to the development of the sea lion as a model for deep-diving physiology. In addition, the limits of a species' physiological response to diving, especially during extreme dives, is key to understanding how the animal may respond to disturbances in the environment (i.e., sound, temperature, prey availability). In this study we will determine the rate and magnitude of O_2 store depletion during dives, and investigate its relationship to heart rate and workload, thereby improving our understanding of O_2 management during diving, specifically the role of lung O_2 stores and O_2 delivery to tissues.

OBJECTIVES

This study will utilize backpack digital recorders to measure blood oxygen depletion, heart rate, and flipper stroke rate in dives of California sea lions during maternal foraging trips to sea from San Nicolas Island. The goals of this research are 1) determination of the rate, pattern and magnitude of blood O_2 store depletion during both shallow and deep dives at sea, 2) documentation of heart rate profiles of shallow and deep dives, and assessment of the relationship between changes in heart rate to blood O_2 profiles, and 3) documentation of flipper stroke rate profiles during shallow and deep dives, and assessment of the relationship of stroke rate to both changes in heart rate and changes in blood O_2 profiles.

APPROACH

Objective 1: In order to calculate the rate and magnitude of depletion of the blood O_2 store during dives, P_{O_2} profiles will be obtained from a P_{O_2} recorder and intravascular electrode deployed on sea lions (McDonald and Ponganis 2012). As in previous research by the PI with California sea lions and other species (McDonald and Ponganis 2013; Meir et al. 2009; Meir and Ponganis 2009), the P_{O_2} profiles will be converted to Hb saturation profiles with the use of the sea lion O_2-Hb dissociation

curve. In addition to the P_{O2} and Hb saturation profile during a dive, the start-of-dive and end-of-dive % Hb saturations can then be used to calculate the magnitude of blood O_2 depletion during dives based on the net change in % Hb saturation, and the known Hb concentration and blood volume.

Objective 2: ECG profiles will be collected from a second group of freely diving lactating female sea lions. The following indices of heart rate during dives will be measured and compared in shallow vs. deep dives: a) dive heart rate (total number of beats / dive duration), b) maximum heart rate during a dive, c) minimum heart rate, d) time into the dive (% of dive duration) until resting heart rate (70 bpm) (Ponganis et al. 1997) is reached, and e) duration of and heart rate during the ascent tachycardia. If possible, heart rate during rest periods will also be measured if females are seen resting on land. Although heart rate will not be measured concurrently with P_{O2} we will compare heart rate and P_{O2} data between dives of similar duration and depth to determine any potential relationship between heart rate and blood O_2 depletion.

Objective 3: Accelerometers will be deployed on females with ECG data loggers in order to evaluate stroke-glide patterns in shallow vs. deep dives and to examine the relationship between heart rate and stroke rate. Although venous P_{O2} will not be measured concurrently with stroke rate, we will compare stroke rate and venous P_{O2} depletion profiles (collected for our previous ONR funded project) between dives of similar duration and depth to determine any potential similarities between stroke rate and venous blood O_2 depletion rate profiles. In addition, we will evaluate whether there is any difference in the relationship of stroke rate vs. venous O_2 depletion in shallow vs. deep dives.

WORK COMPLETED

Analysis of heart rate response during dives to different depths has been published (McDonald and Ponganis 2014). Analyses of stroke rate and minimum specific acceleration (an index of workload) (Simon et al. 2012), and of the relationship of these two variables to heart rate are almost completed. Further documentation of blood oxygen depletion profiles has been obtained. Data are in preparation for manuscripts for publication and for talks for presentation at the upcoming Marine Mammal Conference. In addition, a paper on sea lion anesthesia technique and the relationship of pH to P_{CO2} is in progress. Presentations were made at the Bio-logging Conference in 2014, and at the 2015 Western Anesthesia Resident Conference (US Navy anesthesia resident).

RESULTS

Heart rate data have been completely anlayzed, and published (McDonald and Ponganis 2014). Accelerometer data analysis has progressed with development of stroke identification programs. Review indicates that during deep dives, after initial stroking for 30 seconds, the sea lions primarily glide during descent to depths of 350 to 400 meters, and then gradually stroke at the bottom of the dive and during ascent (Fig. 1). Resting heart rates were 54 ± 6 beats min^{-1} (bpm), and in dives of 1-3 min, 3-5 min, and > 5 min, dive heart rates (number of beats/dive duration) were 55 ± 8, 51 ± 6, and $40 \pm$ bpm. As illustrated in Figs. 1 and 2, the heart rate profile was characterized by rapid development of a bradycardia (slow heart rate), and a gradual increase in heart rate during the bottom phase of the dive and during ascent. The degree of bradycardia was more intense in deeper dives with heart rates as low as 10 bpm during the deepest dives.
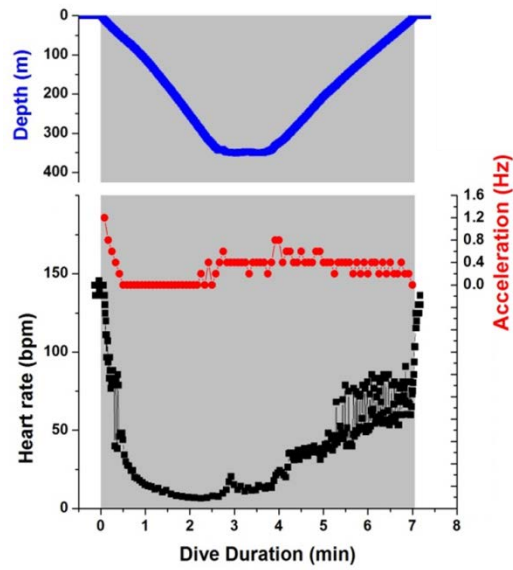
Figure 1. Heart rate (beats per min (bpm)) and stroke rate (acceleration axis in Hertz (Hz)) during a 350-m deep dive of a California sea lion. Note that stroke rate declines to zero by 30 s into the dive and that heart rate reaches 10 bpm in late descent.
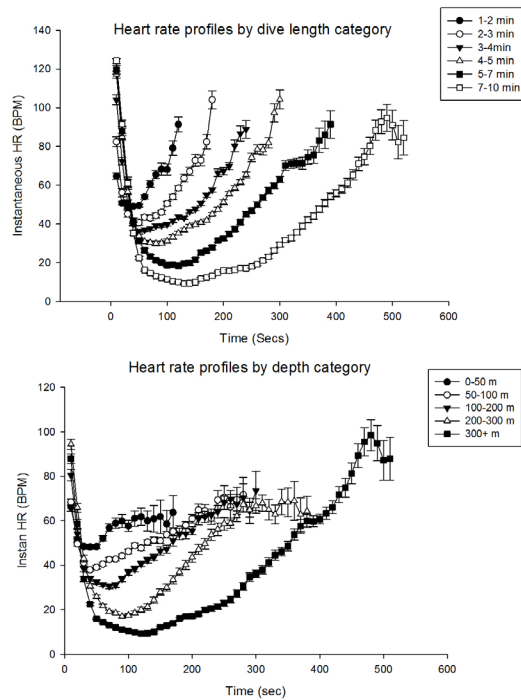

Figure 2. Instantaneous heart rate in 30-sec intervals in dives of different duration and depth categories. Initial heart rates are progressively higher for deeper dives of longer duration, and the degree of bradycardia increases with maximum depth and duration of dives.

Stroke rate data have been analyzed and are in preparation for publication. As illustrated in Fig.2, stroke rates of shallow dives are highly variable, with mean values (determined at 10 sec intervals) ranging from 3 to 18 strokes min[-1.]. In general, slower stroke rates occur at deeper depths. In deep dives (> 200 m), after a few initial strokes, descent is characterized by a prolonged glide to maximum depth, after which stroke rate increases slightly during the bottom phase of the dive, and then, during early descent peaks near 25 strokes min^{-1}, and then gradually declines during final ascent.
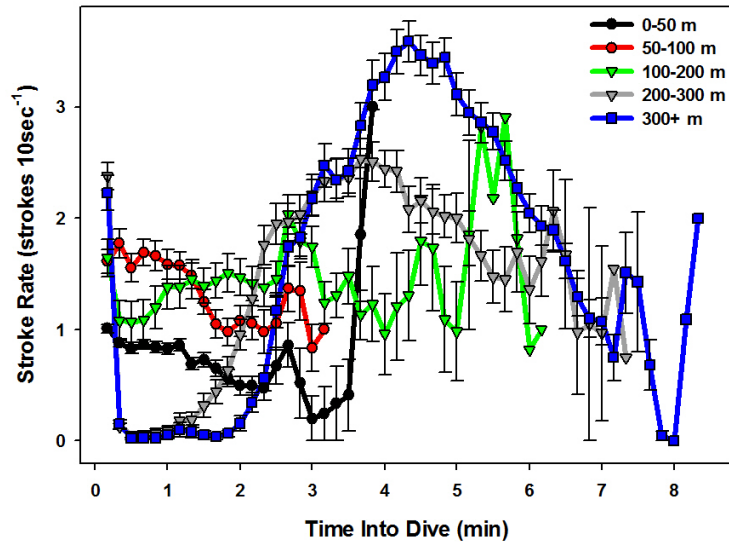

Figure 3. Stroke rate at 10-sec intervals into dives of different depth categories.

Stroke rate analysis and manuscript preparation are in fina progress. Profiles of heart rate, stroke rate, posterior vena caval hemoglobin saturation and arterial saturation during deep dives demonstate the complexity of the relationship between these variables during diving (Fig. 4).
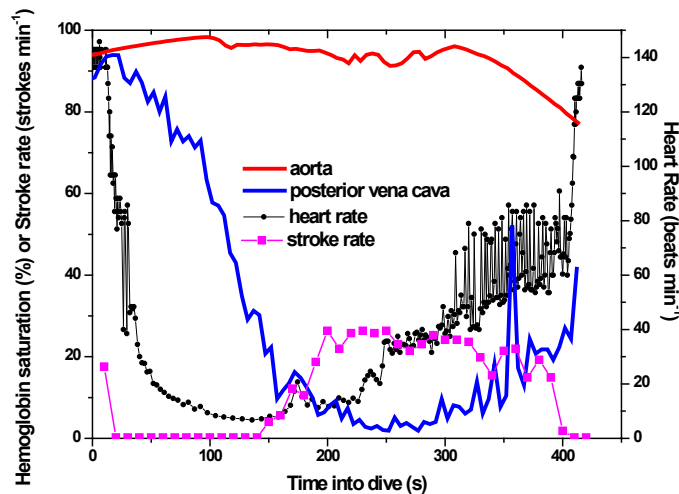

Figure 4. Profiles of arterial and venous hemoglobin saturation, heart rate and stroke rate demonstrate the complexity of physiological responses during deep dives.

In descents of deep dives, heart rate profiles parellel the decline in stroke rate, but throughout the remainder of the dive, a strict relationship is not as apparent. During ascent, the rise in hear rate lags behind that in stroke rate, and then, heart rate continues to increase despite a steady and even declining stroke rate. In addition, the steepest rates of hemoglobin desaturation (during descent) occur when stroke rate is zero; clearly the decline during descent is not due to stroke effort. And during ascent, the saturation rises during periods of higher heart rates and stroke rates.

In addition, minimum specific acceleration (MSA) has been analyzed as another index of muscle workload(Fig. 5). These data provide further evidence that, although heart rate may be influenced by stroke rate during shallow, short duration dives, the heart rate response becomes more and more independent of stroke rate as dive duration and dive depth increase.
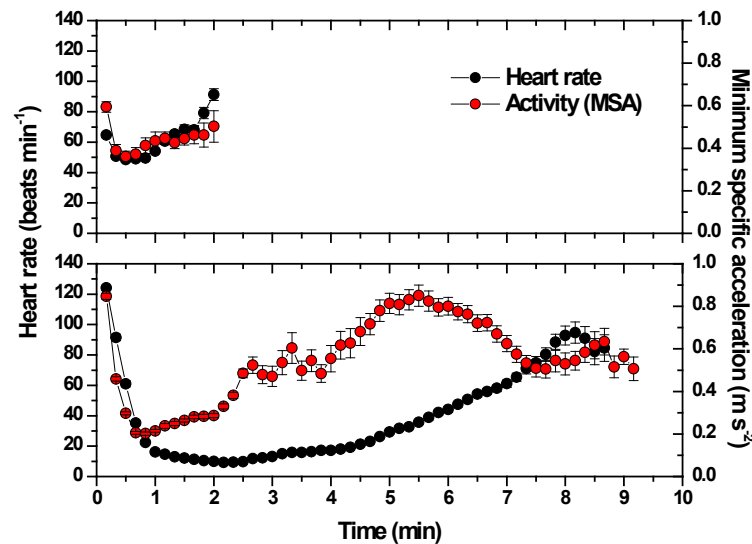

Figure 5. The relationship of heart rate to minimum specific acceleration becomes more independent as dives become deeper and longer.

During shallow dives, higher stroke rates are generally accompanied by higher heart rates, suggesting a stronger link between heart rate and muscle workload during short duration dives. However, their relationship the to the venous blood oxygen profile. However, the relationship of these two variables to the rate of blood oxygen depletion is highly variable. Venous oxygen content can actually increase during short duration dives. This suggests very little muscle blood flow and evven the use of arterio-venous shunts during such dives.

IMPACT/APPLICATIONS

In prior ONR-funded research, partial pressure of oxygen (P_{O2}) profiles provided evidence that lung collapse occurred near 200-m depth in diving sea lions (McDonald and Ponganis 2012). This impairment of gas exchange limits nitrogen uptake at depth and preserves lung oxygen for later use during ascent. Now, this more recent research has revealed that heart rate rapidly declines during descent of deep dives to values less than 10 beats min^{-1} (Fig.1). Such a low heart rate also limits the absorption and distribution of both nitrogen and oxygen at depth (through reductions in pulmonary and aortic blood flow). As a result of these physiological processes, the sea lion can maintain arterial hemoglobin saturation above 90% during deep dives as long as 7 minutes (McDonald and Ponganis

2012; McDonald and Ponganis 2013). In contrast, the elephant seal (*Mirounga angustirostris*), which dives on expiration and has less than 5% of total body O_2 stores in the respiratory system, experiences significant hypoxemia with routine arterial hemoglobin desaturation to 10 to 20% (Meir et al. 2009). However, similar to the sea lion, the emperor penguin (*Aptenodytes forsteri*), another animal that dives on inspiration with a large respiratory O_2 store, also can maintain arterial saturations during dives as long as 10 min (Meir and Ponganis 2009). It is also notable that a severe bradycardia during descent occurs in deep-diving emperor penguins (Wright et al. 2014), and in deep-diving bottlenose dolphins (*Tursiops truncatus*), which also dive on inspiration (Houser et al. 2010; Williams et al. 1999). For these reasons, it is hypothesized that the heart rate profile during deep dives of California sea lions is universal among higher vertebrates that dive on inspiration. Hence, both lung collapse and the heart rate profile make the California sea lion a valuable model to investigate physiological responses and gas uptake / distribution during deep dives.

The lower heart rates during deeper, longer dives observed in this study and the lack of blood oxygen depletion during these deep dives that were documented in our prior ONR study (McDonald and Ponganis 2012; McDonald and Ponganis 2013) also have implications for the management of oxygen stores and the physiological basis of the ADL. The concept that most dives are aerobic in nature and do not exceed an aerobic dive limit (ADL - dive duration associated with the onset of post-dive blood lactate accumulation) has dominated the interpretation of dive behavior and foraging ecology over the past 30 years (Costa et al. 2001; Kooyman et al. 1980). However, because of technical difficulties, the ADL has rarely been measured. Instead, researchers have had to resort to estimations of total O_2 store depletion, i.e., calculated ADLs (cADLs) (Costa et al. 2001; Weise and Costa 2007). Our findings in sea lions support the concept that the physiological basis of the ADL is muscle oxygen depletion and subsequent glycolysis. The lung and blood oxygen stores are not completely depleted in even the longest of sea lion dives. The severe bradycardia during deep dives contributes to the preservation of the blood and lung oxygen for use during ascent, and it also creates greater reliance of muscle metabolism on the myoglobin-bound muscle oxygen store. In addition, the highly variable relationship between heart rate and stroke rate suggests that muscle blood flow and oxygen delivery are not coupled with stroke effort (Figs 1, 4, and 5). These findings reinforce our hypothesis that depletion of the muscle oxygen store with subsequent glycolysis underlies the ADL.

In order to better evaluate the stroke rate – heart rate relationship, and the relation of both of these variables to venous blood O_2 depletion, we are pursuing collection and analysis of simultaneous records of these variables in the newest phase of our ONR-funded research. Documentation of these patterns will establish the deep-diving California sea lion as an excellent model for investigation of physiological responses and blood nitrogen kinetics in a deep-diving marine mammal. As such, the sea lion represents the best available model in which to collect data to understand the physiology and gas kinetics of a deep-diving marine mammal. This is pertinent to the understanding of beaked whale stranding associated with sonar exposure and to the many mathematical models of nitrogen uptake and distribution in these animals (Hooker et al. 2012)

RELATED PROJECTS

This project is building on our findings from our previous ONR funded project "Blood oxygen depletion in California sea lions: How close to the limit?" (award #: N000141010514), and formed the basis for our new ONR grant "Blood oxygen conservation in diving sea lions: How low does oxygen really go?" (N000141410404).

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